Table 3

Frequency, density, and sizes of individuals of species collected at Bird and Turn Rocks, San Juan Islands, Washington, July, 1968.

Species	Frequency				Numbers per m²			Number of Individuals Collected
	Rock	Tide-Pool	Cob-ble	Gravel	Peak	Mean	SD	
Acmaea mitra Rathke, 1833	1	0	0	0	1	1.0	—	1
Calliostoma ligatum (Gould, 1849)	2	2	1	0	1	0.9	0.2	5
Margarites pupillus (Gould, 1841)	7	3	4	0	141	25.1	44.5	357
Lirularia parcipicta (Carpenter, 1864)	1	1	1	0	3	1.7	1.2	5
Lacuna sp.	6	2	3	0	19	7.6	5.9	86
Littorina sitkana Philippi, 1845	14	0	4	0	76	10.6	17.8	152
Littorina scutulata Gould, 1849	15	1	4	0	344	35.4	76.2	500
Bittium eschrichtii (Middendorff, 1849)	0	2	3	2	216	48.0	84.3	121
Odostomia sp.	0	0	0	1	2	2.0	—	1
Ceratostoma foliatum (Gmelin, 1791)	3	0	1	0	2	1.2	0.5	4
Ocenebra interfossa (Carpenter)	2	0	2	2	12	3.7	4.2	16
Thais emarginata (Deshayes, 1839)	9	0	0	0	23	6.1	7.3	62
Thais canaliculata (Duclos, 1832)	14	1	3	1	186	42.5	60.0	805
Thais lamellosa (Gmelin, 1791)	14	3	6	2	99	13.7	23.8	339
Searlesia dira (Reeve, 1846)	4	1	2	1	15	3.9	5.1	28
Amphissa columbiana Dall, 1916	1	0	1	0	3	2.5	0.7	5
Total	93	16	35	9	429			2487
Number of Samples	18	3	6	2				

SD=standard deviation

bottom is within one meter of MLLW in Bahía El Coco, and within 2 - 5 m on Punta Miga.

The tidal range at Playas del Coco is substantial, and the visits included periods of maximum tidal excursion. The mean tidal range at Bahía de Culebra, just north of Playas del Coco, is 7.5 ft. [2.3m] (spring range, 9.0 ft. [2.7m], mean tide level, 4.5 ft. [1.4m]; the corresponding figures for Friday Harbor, Washington, are: mean range, 4.5 ft. [1.4m], diurnal range, 7.7 ft. [2.3m] and mean tide level, 4.8 ft. [1.5m]; ANONYMOUS, 1969). The two low tides of each day are nearly equal (in contrast to the unequal tides at Friday Harbor).

The beach provides a gradient of wave action from moderate to low. The beach is divided by Punta Centinela into an outer exposed portion on Punta Miga, and an inner, sheltered portion in Bahía El Coco. At the head of the Bay the water is generally calm, and much of the intertidal surface is covered by a thin layer of silt (presumably from the Quebrada San Francisco). On more exposed areas, the sea is generally choppy between 10:00 and 16:00, and calm at other times. Both visits were made during the dry season, which, according to local residents, is the roughest time of the year.

FAUNAL DISTRIBUTIONS IN COSTA RICA

The samples included only gastropods (Tables 1 to 4) and do not represent all of the habitats on the beach. More general habitat descriptions can be constructed from available field notes, and these will provide a more complete perspective on actual habitat quality.

The lowest areas in the exposed portion of the beach are covered by a dense growth of small, erect algae (mostly red). The dominant animal of this zone, the urchin *Echinometra*, has eroded much of the zone by constructing burrows. Relatively few gastropods were found in this zone, and no samples were taken from it. The algal cover reaches up to MLLW in the exposed areas, but is not as high within the bay, and only isolated patches of algae are found in the calmest areas. Urchins are also much less common in the bay. In the exposed area, the algal turf covers stones in some places (Samples 13 and 36).

Mid-level rock-reef areas have a sparse coating of the 5 barnacle species that support the major barnacle predators of the site, *Thais melones* and *Acanthina brevidentata*. The most common barnacle is *Chthamalus panamensis*, a relatively small species that forms the major diet of *A.*

Table 4

Characteristics of samples collected on Bird and Turn Rocks, San Juan Island, Washington

Sample Number	Height Class	Height cm	Number of Prosobranch Species[1]		Density[1] per m²
			Total	Common[2]	
		Samples from Rock Habitats			
31D	F	195	4	3	429
51A	E	180	2	2	2.5
25A	E	156	5	2	35
35D	B	90	5	5	158
24A	B	90	4	3	76
32D	B	81	5	5	176
33A	B	66	5	4	18
3D	B	60	2	2	85
8D	A	30	5	4	145
21A	A	30	7	5	22
8A	A	0.0	3	2	8
55D	A	-15	8	6	248
4D	A	-21	6	4	190
21D	A	-21	8	5	62
24C	A	-30	6	6	31
3C	A	-36	7	5	25
28A	A	-30	7	4	21
31A	A	-45	5	5	24
		Samples from Gravel			
32A	A	0.0	4	3	252
4A	A	30	5	3	126
		Samples from Tidepools			
1A	A	0.0	5	2	116
1B	A	-15	7	3	155
51D	A	-15	4	2	59
		Samples from Cobble habitats			
22A	A	15	6	4	133
3A	A	0.0	3	1	77
1D	A	-15	4	3	14
28D	A	15	7	5	207
7A	A	-15	9	6	29
1C	A	-36	6	6	26

Height and exposure classes, see text.
Sample sizes, 2m² (33A, 51A, 7A); 2.5m² (25A), 0.5m² (4A), 0.25m² (32A); others 1m².
A. B, Bird Rock; C, D, Turn Rock.
[1]Excludes limpets other than *Acmaea mitra.*
[2]More than one individual in sample.

brevidentata (Paine, 1966a). At upper shore levels, one finds *Chthamalus imperatrix*. The most common large barnacle on the reef is *Megabalanus peninsularis*, which is relatively uncommon and usually restricted to crevices and other protected sites in the exposed area. One also finds scattered *Tetraclita stalactifera* and *Cataphragmus pilsbryi* Broch, which are probably too large and solid to be used for food by the snails. None of these barnacles settled during the two visits, and none appeared to have settled for some time prior to the visits. In contrast, *Bala-*

nus trigonus Darwin was fairly common in the subtidal areas of the vicinity, and settled in large numbers during February and March, 1970.

Mid-level rock-reef in the calmest areas (near Quebrada San Francisco) is fairly silted and also subject to changing sand levels. In this area, the reef was never more than about 0.5 m above the substrate. Sand-levels dropped about 15 cm during March, 1970; presumably rises would also take place, at times covering the whole reef. The fauna of this precarious area (Samples 8 and 38) is strikingly different from that of the less silted reef only a few meters away. Virtually all of the *Thais biserialis* and *Anachis costellata* were obtained in these 2 samples. The silted reef fauna is similar to that of the mid-bay reef (Figure 1), and also to that at the Gulf of Nicoya site visited by PAINE (1966b).

The rock reefs are dissected by crevices, and these may contain rich faunas of crabs, anemones, tunicates, and sea cucumbers, absent from the barren reef faces. Crevices are an important habitat element, as virtually all lower shore snails move into hiding places during the low-tide periods. Crevices are also important for *Hipponix pilosus* and gastropod prey such as oysters and mussels (in the high intertidal zone) and *Chama* (in the lower intertidal zone).

Cobble areas vary in extent and character, and most of the samples were taken from unique sites. Some stones have rich faunas of sponges or tunicates, or both (Samples 9, 16, 22 and 36). Stones frequently provide hiding places for ophiuroids (Samples 1, 2, 5, 13, 21 and 22), anemones (Samples 1, 3), sea cucumbers (Samples 21, 22), and crabs as well as snails. Stones may sit on silt (Samples 1, 2), sand (Samples 3, 4), coral debris (Samples 5, 19, 21; debris from the dead coral reef indicated in Figure 1), shell and gravel (Sample 22), or on solid rock more or less covered with sand, gravel, shell, or coral (Samples 5, 9, 6). Stones also vary in size, from large (turned more or less with difficulty; Samples 17, 21, and 22) to small (Samples 2, 16) or mixed. Understone faunas are similarly variable (Table 1). Some areas contain only gravel; the few areas of gravel that I examined appeared to be devoid of snails.

Species distributions vary with exposure to wave action, or substrate, or both. *Chama* and *Hipponix pilosus* are both largely restricted to crevices on the exposed areas, but form dense populations on open surfaces of more protected areas. On the other hand, the pulmonate limpets and *Fissurella virescens* are common in exposed areas and relatively rare in protected areas. Substrates also vary along the beach, with sand on the exposed portion, coral debris in the area protected by Centinela, sand deeper in the bay and then silt near the head of the bay.

RESOURCE PARTITIONING BY TROPICAL HERBIVORES

The 6 species of upper-level rock-scraping herbivores with spiral shells belong to 4 genera: *Nerita, Littorina, Fossarus,* and *Planaxis.* In Costa Rica 1 to 2 species were found

Table 5

Distribution of littorine-like snails among beach habitats of Washington and Costa Rica

	Number of samples containing species at various Height (m) and Substrate combinations							
Species	Tide-Pool	Rock >2m	Rock 1-2m	Rock Silt 1-2m	Rock Other	Stone 0-1.5m	Stone 1.5-2m	Stone Other
				Costa Rica				
Nerita funiculata	2	0	0	2	2	8	1	0
Nerita scabricosta	1	3	0	0	0	0	1	0
Littorina aspera	0	3	0	0	0	0	0	0
Littorina modesta	0	2	0	0	0	0	0	0
Fossarus sp.	2	1	0	2	0	0	0	0
Planaxis planicostatus	1	0	0	0	0	0	2	0
Number of samples	3	3	1	2	8	11	2	4
				Washington				
Littorina scutulata	1	2	3	–	10	–	–	4
Littorina sitkana	0	1	3	–	10	–	–	4
Number of samples	3	2	3	0	13	0	0	6

in most samples (10 samples contained 1 species, 7 samples 2 species, 1 sample 3 species, 1 sample 4 species, and 10 samples no species).

The distribution of each species can be described in terms of height and substrate. On rock reef areas above 2 m, *Littorina aspera* and *Nerita scabricosta* are generally found together; between 1 m and 2 m (except in the silted area) one finds *L. modesta* and *Fossarus* sp. (no samples were taken from this portion of the beach; sample 12, within this height range, was at the exposed front of the reef and included an entirely different fauna). *Nerita funiculata* occupies cobble between 0.3 m and 1.5 m, usually without another of these species, and also rock reef areas between 1 and 2 m in the silted area, where *Fossarus* sp. is also found. *Planaxis planicostatus* occupies the remaining mid-level environment, cobble between 1.5 and 2 m, together with occasional *Nerita* (Sample 4 contained 21 *N. funiculata* and Sample 26, 2 *N. scabricosta*, as opposed to 1120 and 88 *P. planicostatus*, respectively). The quantitative samples show the abruptness of these distributions (Table 5).

The resource partitioning by the Costa Rican snails is in contrast to habitat usage in Washington. There, only 2 species, *Littorina scutulata* and *L. sitkana* are found, and both species are found throughout the beach (together in 16 samples, separate in 6, and missing from only 2 samples). The greater diversity of the tropical site is accompanied by a finer division of the upper shore habitat, but individual habitat patches do not support more species.

FEEDING OBSERVATIONS

Although no systematic studies of food habits were undertaken, I did encounter a number of feeding animals during the study period. Most snails are hidden during the day, and become active at night. Feeding was observed only during late afternoon or night tides. For most species only a single observation was made and, therefore, the observed prey may not be a major diet item (for example, see Paine, 1966a, 1966b; Miller, 1974). *Muricanthus princeps* fed on *Chama*, *Opeatostoma pseudodon* on *Chthamalus*, *Thais speciosa* on *Cerithium*, and *Thais melones* on *Chama* and *Megabalanus peninsularis.* Often several *Th. melones* were observed feeding on the same *Chama.* Some of the columbellids were attracted to and began feeding on freshly killed crabs, limpets, and chitons while samples were being sorted in the laboratory (*Mitrella delicata, M. guttata, Anachis pygmaea, A. nigricans*). *Anachis pygmaea* and *A. lentiginosa* occurred together in 10 of 15 samples. These 2 species form dense populations; they hide under stones during the day and migrate to the top at night. The 2 species are approximately equally represented (for example, from one rock, 65 *A. lentiginosa* to 43 *A. pygmaea*). However, in the laboratory, the 2 species responded entirely differently to freshly killed animals; the *A. pygmaea* were quickly attracted, while the *A. lentiginosa* were not.

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Literature Cited

Anonymous
1969. Tide tables west coast of North and South America including the Hawaiian Islands. U. S. Dept. Comm., Coast & Geodet. Surv. 226 pp.

Dayton, Paul K.
1971. Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41: 351 - 389; 17 text figs.

Johnson, Ralph Gordon
1970. Variations in diversity within benthic marine communities. Amer. Natural. 104: 285 - 300

Keen, A. Myra
1971. Sea shells of tropical West America: marine mollusks from Baja California to Peru. Stanford Univ. Press, Stanford, Calif. i - xiv + 1066 pp.; ca. 4000 figs.; 22 color plts. (1 September 1971)

Kozloff, Eugene
1973. Seashore life of Puget Sound, the Strait of Georgia, and the San Juan Archipelago. Univ. Wash. Press, Seattle, Wash.; 282 pp.; 28 plts.; 223 figs.

Miller, Alan Charles
1974. A comparison of gastropod species diversity and trophic structure in the rocky intertidal zone of the temperate and tropical West Americas. Ph. D. thesis, Univ. Oregon, 143 pp.; 10 figs.

Paine, Robert Treat
1966a. Function of labial spines, composition of diet, and size of certain marine gastropods. The Veliger 9 (1): 17 - 24; 2 text figs. (1 July 1966)
1966b. Food web complexity and species diversity. Amer. Natural. 100: 65 - 75; 2 figs.

Ricketts, Edward F., Jack Calvin & Joel W. Hedgpeth
1968. Between Pacific tides. Stanford Univ. Press, Stanford, Calif. v - xiii + 3 - 502; 46 plts.

Vance, Richard R.
1972. Competition and mechanism of coexistence in three sympatric species of intertidal hermit crabs. Ecology 53: 1062 - 1074; 12 figs.